CERCARIA DIPTEROCERCA MILLER AND NORTHUP, 1926 AND STEPHANOSTOMUM DENTATUM (LINTON, 1900) MANTER, 1931 [1]

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After a preliminary survey had shown that *Nassa obsoleta* is the most heavily parasitized gastropod in the Woods Hole region, Miller and Northup (1926) reported on a study conducted for one year to determine seasonal infection of this snail by larval trematodes. They examined 8875 individuals, first by isolation for 48 hours to determine those from which mature cercariae were emerging, and subsequently by crushing the snails individually and examining the tissues under a binocular microscope for infection by the asexual generations. They recorded total and seasonal infection by five species, all described as new to science, and named *Cercaria setiferoides, Cercaria quissetensis, Cercaria variglandis, Cercaria dipterocerca,* and *Cercariaeum lintoni.* The last species had been described but not named by Linton (1915).

Later studies have traced the life-cycles and systematic relations of these cercariae. Martin (1938) showed that *C. setiferoides* encysts in turbellarians and spionid annelids and becomes mature in the sand-dab, *Hippoglossoides platessoides,* and small flounders (not specifically identified but probably *Pseudopleuronectes americanus* or *Paralichthys dentatus*). The adults were described as *Lepocreadium setiferoides* (Miller and Northup). Stunkard (1938a) worked out the life-cycle of *C. quissetensis;* the cercariae encyst in marine mollusks and become sexually mature in the herring gull, *Larus argentatus.* They were described as *Himasthla quissetensis* (Miller and Northup, 1926). Stunkard (1938b) found that *C. lintoni* had been described and named *Distomum lasium* by Leidy (1891); that the metacercariae encyst in polychaete annelids and mature in fishes. The worms were assigned to *Zoogonus rubellus* (Olsson, 1898) Odhner, 1902, but after study of the European species, whose metacercariae were found in sea-urchins, Stunkard (1941) recognized bionomic and morphological differences between the European and American species and listed the adults of *C. lintoni* as *Zoogonus lasius* (Leidy, 1891). Stunkard and Hinchliffe (1952) discovered that *C. variglandis* is the causative agent of "swimmers' itch" of oceanic beaches in New England and the adults proved to be identical with avian blood-flukes that had been described by Price (1929) as *Microbilharzia chapini.* Penner (1953) suppressed *Microbilharzia* as a synonym of *Austrobilharzia* Johnston, 1917 and listed the species as *Austrobilharzia variglandis* (Miller and Northup, 1926). The fifth species, *Cercaria*

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stomach of *Lophius piscatorius* which also contained two partially digested specimens of the dab, *Limanda ferruginea*.

Other encysted larvae from various parts of the world have been referred to *Stephanostomum* on the ground of morphological similarity but without experimental confirmation. They were found in Britain by Johnstone (1905), Lebour (1908), Nicoll and Small (1909) and Nicoll (1910); in Ceylon by Lühe (1906), in Japan by Yamaguti (1934, 1937) and in Florida by Sogandares-Bernal and Hutton (1959a). Martin (1939) reported the first experimentally demonstrated life-cycle in the genus. He showed that sticky-tailed, stylet-bearing, ocellate cercariae from rediae in *Nassa obsoleta* encyst and develop to metacercariae in the mesenteries and liver of *Menidia (Menidia) notata* and continue development to nearly mature adult worms in the intestine of young puffers, *Spheroides maculatus*. The worms were identified as *Stephanostomum tenue* (Linton, 1898) Martin, 1938, a species described originally from the striped bass, *Roccus lineatus*, at Woods Hole, Massachusetts, and subsequently (Linton, 1940) from the sand-launce (*Ammodytes americanus*), the sea-raven (*Hemitripterus americanus*), the kingfish (*Menticirrhus saxatilis*), the white perch (*Morone americana*), the striped bass (*Roccus saxatilis*), and the toadfish (*Opsanus tau*). Margarita Bravo (1956) reported *S. tenue* from the intestine of *Trachurops crumenophthalma* taken on the Pacific coast of Mexico.

The life-cycle of a second species, *Stephanostomum baccatum*, was reported by Wolfgang (1954, 1955a). According to the report, ophthalmoxiphidiocercous cercariae, "secondarily" lacking stylets, develop in rediae in *Buccinum undatum* and *Neptunea decemcostatum*, encyst as metacercariae in the skin and somatic muscles of pleuronectid fishes and occur as adults in the rectum of *Hemitripterus americanus* and other fishes. A description was given of all stages in the cycle but there are disturbing inconsistencies in the account which may invalidate the conclusions. *Stephanochasmus baccatus* (= *Stephanostomum baccatum*) was described by Nicoll (1907) on a single specimen from the intestine of *Hippoglossus hippoglossus*. The description was adequate to validate the species and was supported by a good figure. The species was reported by Manter (1926) from the same host taken at Mount Desert Island, Maine. Stafford (1904) recorded *Stephanostomum sobrinum* (Levinsen, 1881) Looss, 1901 from the sea-raven (*Hemitripterus americanus*), the arctic eelpout (*Lycodes* sp.), and the wrymouth (*Cryptoacanthodes maculatus*). Caballero (1952) intimated that the specimens are probably not identical with *S. sobrinum* and suggested that they may belong to *S. tenue*. After examination of Stafford's specimens, Wolfgang (1955a) stated that they are *S. baccatum*. Wolfgang studied approximately 1000 specimens, taken from a variety of hosts, but data from literature and from observation are intermingled and frequently it is difficult if not impossible to distinguish between them. He reported the worms from the lower intestine and rectum and listed as final hosts the three species named by Stafford and also *H. hippoglossus* and the short-horned sculpin (*Myoxocephalus scorpius*). The distribution of the parasite was given as across the North Atlantic Ocean from Maine to Nova Scotia, Newfoundland, Greenland and the North Sea coast of Europe. But Wolfgang was doubtful of the validity of *S. baccatum* since he stated (1955a, p. 119), "Levinsen inadequately described *S. sobrinum* from *Cottus scorpius* in Greenland waters, and Odhner (1905) reported but did not redescribe it from the same host in unspecified arctic waters. Although Levinsen's description of *S. sobrinum* is vague it agrees essentially with that of *S. baccatum*. In view of the hosts and the distribution of the parasite, *S. sobrinum* and *S. baccatum* are probably conspecific." Stafford may have been correct in his determination and if the two species are identical, *S. baccatum* disappears as a synonym of *S. sobrinum*. Furthermore, Wolfgang stated (1955b, p. 135), "that *S. baccatum* shows no valid differences from *S. triglae*." If these species are conspecific, *S. triglae* Lebour, 1908 also would be suppressed as a synonym.

Although Wolfgang gave descriptions of the successive stages in the life-cycle of *S. baccatum,* there is no assurance that the cycle was actually completed in experimental hosts. The methods were so lacking in control that opportunity for confusion was obvious. There is virtually no evidence that the cercariae taken by dissection from *Buccinum undatum* and *Neptunea decemcostatum* develop into the metacercariae found encysted in the flounders. Moreover, proof of the identity of the metacercariae encysted in winter flounders, *Pseudopleuronectes americanus,* and the adults of *S. baccatum* was based on infections resulting from the following procedure, (1954, p. 965), "Gelatin capsules were filled with cysts taken from fins and muscles of the winter flounder and placed in the siphons of clams which were then fed to the fish." The author admitted (p. 965), "Although several hundred cysts were used for each dose, no comparison between numbers of cysts introduced into experimental hosts and numbers of adult worms recovered could be made because their viability may have been impaired by dissection." But the cysts of *Stephanostomum* are so tough and resistant that it is difficult to see how the infectivity of the larvae could be impaired during dissection. Furthermore, it is apparent from the report that the fishes used for experiment were already infected and as many as 567 worms were taken from a sea-raven collected near Clam Cove, Deer Island, N. B. The data presented in Table I (1954, p. 966) show that after feeding several hundred cysts in each dose, the heaviest infection (123 adult worms) was found in a sea-raven dissected four days after feeding, at which time the metacercariae of experimental infection would not yet be adult, and that the number of adult worms decreased with the length of time after feeding to a single worm in an eelpout after twenty-two days, the longest time recorded. These data strongly suggest that natural infections harbored by the experimental fishes were gradually lost during captivity and there is no proof that the worms recovered at autopsy were derived from the cysts that had been fed in the experiment. But the most disturbing inconsistencies are found in the morphological section of the paper. As described, the cercariae show no significant differences from *C. neptuneae* Lebour, 1912 from the same and related hosts, and the two may be identical. An excretory duct is described as extending posteriad from the bladder and terminating in a pore at the tip of the tail. Such a condition is so unusual in a cercaria of this type that the observation is open to question. Moreover, in the cercaria the excretory collecting ducts are portrayed as mesostomate, *i.e.*, they bifurcate behind the acetabulum to give rise to anterior and posterior branches, whereas in the metacercaria they are represented as stenostomate, extending forward without branching to the level of the eye-spots. The latter condition is characteristic of species in the genus *Stephanostomum*. If the descriptions are correct, it is obvious that the cercaria and metacercaria belong to different taxonomic groups and can not be stages in the life-cycle of a single species.

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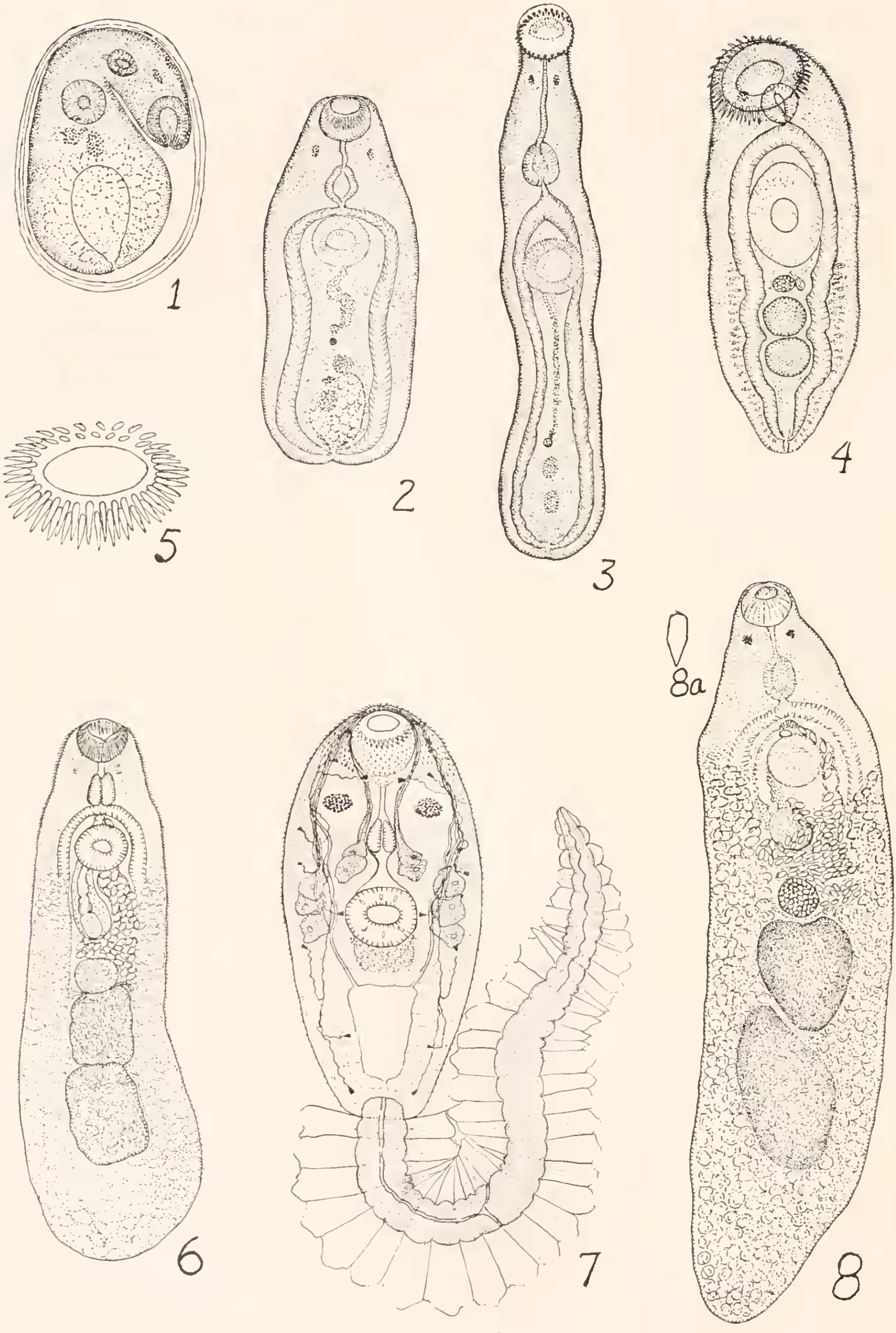

Figures 1–8a.

MATERIAL AND METHODS

Nassa obsoleta, collected in the Woods Hole area, were isolated to find those which were shedding *Cercaria dipterocerca*. The incidence of infection was about 0.2% of the snails taken at the Sheep-Pen Cove on Nonamesset Island; less at other places. Miller and Northup (1926) reported a total of only four infections in the examination of 8875 snails collected at Quisset harbor. When snails are kept for long periods in fingerbowls, the number of cercariae released each day gradually diminishes, and after 12 to 16 weeks shedding may be stopped completely. But although reproduction of the parasite slows down or ceases temporarily, the infection remains in dormant condition and becomes active when the snail again has an abundance of food. It appears that a parasitized snail carries the infection indefinitely and that the parasite undergoes periods of interrupted activity during the winter or whenever the mollusk lacks sufficient nourishment to maintain both its basic metabolism and reproduction of the parasite.

Since the cercariae are provided with penetration glands, they were added to small aquaria with possible invertebrate and vertebrate hosts. They invaded small *Fundulus heteroclitus* and *Menidia menidia* but the fishes often harbored natural infections which could be confused with experimental ones. Dr. Evelyn Shaw reared *M. menidia* from eggs at the Marine Biological Laboratory, and kindly provided small fishes that had not been exposed to infection and therefore afforded absolute control of the experiments. Grateful acknowledgment is made here to Dr. Shaw. The small fishes were fed brine shrimp, *Artemia salina*. The cercariae penetrated the tissues and encysted in the throat, in the mesenteries and in the liver. They were found also under the skin and in the muscles, but the cysts were chiefly in the viscera and apparently the cercariae were taken into the mouths of the fishes with water for respiration. Dissection of these *M. menidia*

FIGURE 1. Metacercaria, in cyst 0.28 mm. long, from laboratory-reared *Menidia menidia*, exposed to *Cercaria dipterocerca*.

FIGURE 2. Metacercaria, from laboratory-reared *M. menidia* exposed to *C. dipterocerca*, released from cyst and pressed to study excretory system; worm as fixed, stained and mounted is 0.62 mm. long. This worm has 54 peristomial spines.

FIGURE 3. Metacercaria, identified as *Stephanostomum tenue*, released from cyst from naturally infected *Fundulus heteroclitus*, Woods Hole, Mass. Specimen fixed, stained and mounted is 1.69 mm. long. This worm has 42 peristomial spines; compared with Figure 2, note length of prepharynx and location of gonads.

FIGURE 4. Smallest of 12 worms on slide No. 8199, Helminthological Collection, U. S. Nat. Museum. Material of *Stephanostomum dentatum* collected 6 October 1911 by Vinal Edwards from *Paralichthys dentatus* at Woods Hole, Mass., ventral view. The worm is somewhat contracted, the anterior end curved ventrally and as mounted is 0.70 mm. long. This worm has 54 peristomial spines.

FIGURE 5. The peristomial spines of the largest specimen, 2.31 mm. long, on slide No. 8199, Helminth. Coll., U. S. Nat. Museum. This worm has 54 peristomial spines.

FIGURE 6. The largest specimen collected by the writer, *S. dentatum* from *P. dentatus*, at Woods Hole. Fixed under coverglass pressure, stained and mounted, it is 2.79 mm. long.

FIGURE 7. *Cercaria dipterocerca*, from *Nassa obsoleta*, ventral view, the portion of the excretory system in the tail undergoing regression.

FIGURE 8. Specimen, 3.5 mm. long, on slide No. 8200, Helminth. Coll., U. S. Nat. Museum. Collected 5 September 1919 from *P. dentatus;* identified as *S. dentatum* and figured in Linton (1940), Plate 3, Figure 25. Only a few peristomial spines remain; they are broad, flat, scale-like.

FIGURE 8a. Peristomial spine from worm shown in Figure 8.

at intervals during the ensuing six weeks yielded a series of developing metacercariae, from recently encysted larvae to mature specimens indistinguishable from those found in natural infections of *M. menidia* and *F. heteroclitus* taken in the Woods Hole area. Most of the natural infections, however, were *Stephanostomum tenue* (Fig. 3) which can be distinguished from *S. dentatum* because the circumoral spines are fewer in number and different in shape. Other differences are apparent from comparison of Figures 2 and 3.

Juvenile and adult specimens of *S. dentatum* have been found as natural infections of *Paralichthys dentatus* taken at Woods Hole. Small and medium sized representatives of this species have been kept for several weeks in the laboratory. But attempts to infect final hosts, *P. dentatus* and other flatfish, have so far not been successful, since the fishes have consistently refused to eat in the aquaria. When a larger aquarium with colder water is available, it should be possible to complete the study and obtain experimental infection of final hosts that had been held in a control tank for several weeks to insure that all worms of natural infection would be sexually mature and that those of experimental infection could be positively identified. Experimental infection of the snail host must await a supply of eggs and miracidia from infected fishes.

Study of the specimens of *Stephanostomum* on deposit in the Helminthological Collection of the U. S. National Museum was afforded through the kindness of Dr. Allen McIntosh, to whom grateful acknowledgment is made. Many of the worms were not suitable for specific identification, but slide No. 8199 contained twelve specimens of *S. dentatum*, collected October 6, 1911, by Vinal Edwards from *Paralichthys dentatus* at Woods Hole, Massachusetts. The specimens ranged from juvenile worms (Fig. 4) to fully mature, gravid individuals, and provided opportunity for comparison of these worms with metacercariae recovered from experimental hosts after exposure to *Cercaria dipterocerca*.

DESCRIPTIONS

Cercaria dipterocerca

Redia

The rediae were described briefly and figured by Miller and Northup (1926). The hemal sinuses of the snail frequently contain scores of small rediae 0.10 to 0.20 mm. in length, similar to the one shown in Figure 4 of Miller and Northup. In these small rediae the body is colorless, the pharynx 0.02 to 0.03 mm. in diameter, the digestive cecum is saccate, about one-half the length of the body, and frequently it contains orange-colored droplets. These larvae are very mobile, moving easily by alternate contractions of annular and longitudinal muscles, anchoring one region of the body while advancing another. There are no feet, specialized portions of the body-wall, which may be protruded to serve as holdfasts. Discovery of a small redia with a contained daughter-redia demonstrates more than one redial generation and the large number of small rediae suggests repeated generations of daughter-rediae.

Larger rediae, containing germ-balls and one or more cercariae, measure 0.25 to 0.75 mm. in length and 0.07 to 0.14 mm. in width. Old ones, empty except for a few germ-balls, are seen occasionally; they may measure up to 1.25

mm. in length, with long, pointed, posterior ends. The average measurement given by Miller and Northup is larger than found in the present study and may have been made on specimens under considerable coverglass pressure. In general, the rediae are oval to cylindrical, often attenuated at one or both ends. Frequently the anterior end is prolonged by a long, slender, neck-like region, about one-half the diameter of the succeeding portion of the body. Contraction of circular muscles may produce an annulate appearance or the formation of two or more wider regions separated by narrower ones. The pharynx is oval to spherical and 0.025 to 0.048 mm. in diameter; its wall is about 0.011 mm. thick. With increasing size and the maturity of increasing numbers of cercariae, the digestive ceca become relatively shorter, the body-walls become stretched and thinner, and the rediae less active. The wall contains yellow to orange droplets, one to four microns in diameter, usually associated in larger oval or circular masses, ten to fifteen microns in diameter. These masses easily dissociate. The cecum contains material, orange to greenish to blackish in color. A birth pore is present, located about the length of the pharynx behind that sucker. The cercariae move about freely in the cavity of the redia.

Cercaria (Figure 7)

Examination of unstained living specimens and others, after staining with vital dyes and after fixation, staining and mounting as permanent preparations, confirms the original description in large part and adds details of the excretory system. The two pairs of glands which stain with neutral red, situated lateral and posterior to the pharynx, were observed. There are apparently three, rather than four, penetration glands situated at either side of the acetabulum. The cells are lobed and partially overlap one another, which renders delineation difficult. Only three ducts were identified although ducts, when empty, are not visible. The cells of the third group, labelled *C* in the figure of Miller and Northup, were not observed.

Bodies of normally emerged cercariae, fixed without pressure in swirling, hot Duboscq-Brasil fluid and stained with Semichon technique, measure 0.135 to 0.145 mm. in length and 0.046 to 0.053 mm. in width. The tails are 0.220 to 0.240 mm. in length and 0.016 to 0.020 mm. wide at the base. The acetabulum is 0.023 to 0.024 mm. in diameter; the oral sucker is slightly larger, 0.024 to 0.025 mm. in diameter; the pharynx is oval to pyriform, usually wider posteriorly, 0.01 to 0.014 mm. in diameter; and the ceca are not developed. Above and behind the acetabulum there is a mass of deeply staining germinal cells, rudiments of the reproductive organs and ducts.

Young cercariae in rediae lack spines, there are no membranous fins on the tail, the ocelli are small and the two excretory pores on the sides of the tail are clearly visible. Indeed, in very young specimens the excretory ducts are not fused in the base of the tail. In such specimens the acetabulum is situated more posteriorly, about one-fourth of the body length from the posterior end; it gradually is moved anteriad as the postacetabular portion of the larva grows faster than the anterior portion.

Normally emerged cercariae are photonegative; they swim rapidly, tail in advance, with the body bent ventrally. The body may extend to a length of 0.240

mm. with a corresponding reduction in width. The tail is subterminal in attachment; it may be extended to a length of 0.340 mm. and the tip may be protruded as a small papilla. The central portion of the tail is 0.018 to 0.025 mm. wide near the base and the lateral cuticular fins are about the same width. The lateral fins have 30 to 36 undulatory plications, the crests of which may simulate setae. The median fin is narrower than the lateral ones; it extends along the ventral side of the distal one-fourth of the tail and forward for about one-third of that distance on the dorsal side. In a fixed and stained specimen, 44 nuclei were counted in the tail. The cuticula of the body, but not of the tail, is covered with spines. There is a narrow spineless area around the mouth and then two rows of alternating peristomial spines, typically 27 in each row. Behind these collar-spines the spines are slightly recurved with broad bases, gradually becoming narrower and smaller posteriorly. There is a pair of conspicuous ocelli or eye-spots, 0.009 to 0.012 mm. in diameter, situated above the lateral ends of the commissure of the nervous system. A very large number of pigment granules surrounds each lenticular cup. When the body is extended, the ocelli are circular but when it is retracted the ocelli are oval, wider than long.

The excretory vesicle is V-shaped when filled and Y-shaped with short arms when empty. It has a definite epithelial wall and is surrounded by cystogenous cells. It is formed by the coalescence and fusion of the excretory ducts of each side, although in young cercariae the two ducts are distinct and open on the sides of the tail, some one-fourth to one-fifth of its length from the base. The ducts in the tail subsequently fuse and regress, so that in emerged cercariae there may be only lateral excretory pores at the junction of the body and tail. The collecting ducts pass forward, ventral to the ducts of the penetration glands, from the anterolateral faces of the excretory vesicle to the level of the ocelli where they turn backward and each gives off a branch which runs in front of the ocellus and divides into three capillaries that drain the three flame-cells situated in the region of the oral sucker. The recurrent tubule passes backward and gives off a second branch that divides to supply the three flame-cells in the preacetabular and acetabular area and then continues posteriad to break up into three capillaries that drain three flame-cells in the postacetabular area. There are tufts of long cilia in the collecting ducts; movement of particles can often be seen in the capillaries and collecting ducts and the emergence of fluid from the excretory pores occurs regularly. There is no reason to doubt the distal movement of fluid in the excretory system. It may be osmoregulatory but the flow of fluid undoubtedly removes nitrogenous waste products from the body.

Development of the cercariae has been studied in serial sections of infected snails. In the morula stage of cercarial embryos a cluster of somewhat larger and more deeply staining cells is visible near the middle of the embryo. These cells are germinal and eventually give rise to the gonads, the vitellaria and the reproductive ducts. But I have not been able with certainty to determine the origin of the cells that form the epithelial wall of the excretory vesicle.

Metacercaria (Figures 1 and 2)

The cercariae encyst soon after they enter the tissues of the fish. Recently formed cysts are oval, each slightly longer than the body of the cercaria, which lies in a fluid-filled cavity. As development proceeds the larva increases in size and is bent ventrally. At first the wall is thin and flexible but it thickens, hardens and becomes very tough. The cyst shown in Figure 1 from a laboratory-reared *M. menidia,* dissected six weeks after exposure to cercariae, measures 0.28 by 0.20 mm. and the wall is 0.015 to 0.020 mm. thick. The largest cyst measured 0.37 by 0.27 mm. The cysts are not strongly enclosed by connective tissue and often drop out, especially in the pharyngeal region, as dissection is made. Released from cysts, young worms are 0.30 to 0.60 mm. in length. The specimen shown in Figure 2, fixed under coverglass pressure, is 0.62 mm. long. As development proceeds, the ocelli regress, the peristomial spines attain a length of 0.025 mm. and a width of 0.004 mm. The acetabulum and oral sucker are almost the same size, about 0.090 mm. in diameter. The pharynx, situated just anterior to the bifurcation of the digestive system, measures 0.036 to 0.043 mm. in diameter. The gonads are clearly outlined and the reproductive ducts are indicated by strands of deeply staining cells. The intestine contains small spherules, 0.005 to 0.007 mm. in diameter. The excretory vesicle is filled with minute spherules about 0.001 mm. in diameter, which render the bladder opaque and give the fluid a milky appearance when expelled.

Stephanostomum dentatum

Adult (Figures 4, 5 and 6)

Although evidence is yet lacking to prove that *Cercaria dipterocerca* is the larval stage of *Stephanostomum dentatum,* morphological agreement supports the probability that the two are conspecific.

Linton (1900) gave a brief but diagnostic description and figures of this species. The worm from *Paralichthys dentatus,* described in that paper as *Distomum* sp. and represented on Plate 40, Figures 73, 74, and 75, is probably a specimen of *S. dentatum* from which the peristomial spines had been lost. Forty years later, Linton (1940) gave a record of collections and restated the diagnostic characters of *S. dentatum.* He determined the number of peristomial spines as 54, their length as about 0.050 mm.; he reported that they are nearly uniform in diameter for the basal half of their length, then taper gradually to the tip, which is sharply pointed. He noted the frequent loss of spines from both the peristomial rows and the general body-surface. He recognized that the mass of spermatozoa in the female duct is in the initial portion of the uterus, not in a seminal vesicle. The largest measured specimens were 2.80 mm. long by 0.100 mm. wide and 2.91 mm. long by 0.77 mm. wide. Specimens deposited in the Helminthological Collection of the U. S. National Museum are mounted on two slides which bear the numbers 8199 and 8200. Slide No. 8199 bears twelve specimens collected October 6, 1911, by Vinal Edwards. The largest worm is 2.31 mm. long and 0.81 mm. wide. The entire surface of the body is spined and the circumoral spines (shown in Figure 5) are clearly 54 in number. This specimen is designated as type of *S. dentatum.* The smallest worm, shown in Figure 4, is 0.70 mm. long; another, 0.94 mm. long, has no eggs in the uterus, and one 1.06 mm. long contains several eggs. The specimen shown by Linton (1900; Plate 39, Fig. 64) contains eggs. According to the legend the figure is × 100, and since it measures only 80 mm., the worm was less than 1.00 mm. long. The largest specimen collected during the present investigation, fixed under coverglass pressure and shown in Figure 6, measures 2.79 mm. in length. It is clear that the worms become gravid at a length of about 1.00 mm. and most of them when stained and mounted do not exceed 2.00 mm. in length.

The single specimen on Slide 8200, Helminth. Coll., collected September 5, 1919, presumably by Professor Linton, and figured in his (1940) paper (Plate 3, Fig. 25) as a representative of *S. dentatum*, measures 3.50 mm. in length and is shown in Figure 8 and 8a. All the spines, except for a few peristomial ones, have been lost and vestiges of the eye-spots remain. The sockets of certain of the peristomial spines are visible and the few spines which remain are broad, flat (Fig. 8a), and taper abruptly to sharp points. They are 0.045 to 0.050 mm. in length. While the over-all morphology is that of *Stephanostomum*, the vestiges of ocellar pigment indicate that the specimen is young, and two features, its size and the shape of the peristomial spines, denote that it is not *S. dentatum*. It probably represents an as yet unrecognized and unnamed species.

Linton (1905) reported *S. dentatum* from seven host species: *Coryphaena equisetis, Lophopsetta maculata, Micropogon undulatus, Paralichthys albiguttus, Paralichthys dentatus, Pomatomus saltatrix,* and *Rachycentron canadus,* at Beaufort, North Carolina. Manter (1931) listed *S. dentatum* as a common parasite of *P. dentatus* at Beaufort, but he (1947) reported that some of the specimens of Linton were not suitable for identification and that *S. dentatum* seems characteristically to be a parasite of flounders. In this paper, Manter (1947) reported *S. dentatum* from the marine fishes, *Epinepheles adscencionis, Epinepheles morio* and *Mycteroperca venenosa* at Tortugas, Florida. But the material consisted of only three specimens and a fragment that lacked both tips. He noted that in the specimens from Florida the gonads were separated and the intervals between them contained vitelline follicles, whereas in the specimens from Beaufort the gonads were close together and not separated by vitellaria. Since this appeared to be a constant character, he suggested that additional material might justify a new species for the Tortugas specimens. In the worm from *E. adscencionis*, shown in his Figure 61, the gonads are smaller and situated more posteriad than in specimens of *S. dentatum* (compare with Figure 6 in this paper). In the Florida material, the separateness of the gonads may be correlated with their smaller size, which permitted extension of the vitellaria into areas between them. The smaller size of the gonads may be due to genetic factors or to development in unusual hosts, or indeed, the worms may not be normal parasites of the fishes in which they were found; instead, they may have been ingested in other hosts. Digenetic trematodes of fishes may persist for some time in the digestive tract of predators and such a possibility should be considered when dealing with instances where the worms are irregular in occurrence or few in number.

Certain morphological details may be added to earlier descriptions. In unpressed specimens the body, especially the postacetabular region, is almost circular in cross-section. The prepharyngeal region, when elongated, is slender, which gives the oral sucker a funnel-like or bell-shaped appearance. In young specimens, before the vitelline follicles develop, the connections between the intestinal ceca and the excretory vesicle to form the uroproct are easily seen. The peristomial spines (Fig. 5) are slightly longer than 0.050 mm. The gonads are almost if not quite contiguous and frequently overlap, the ovary is situated slightly on the right side, the anterior testis sometimes slightly left. The seminal vesicle is followed by a prostatic portion of the male duct and both the cirrus and metraterm bear minute spines. The cirrus is protrusible and in one specimen measures 0.19 mm. long and 0.08 mm. wide.

Discussion

The tendency for members of *Stephanostomum* to lose cuticular spines has led to confusion and taxonomic difficulties as noted by Pratt (1916), Manter (1934) and other authors. Attempts to correlate particular larval and adult stages have not been fruitful, although the taxonomic problems, identity and number of valid species, and systematic position of the genus will not be finally resolved until life-cycle data are available.

Differences in the accounts of Martin (1939) and Wolfgang (1954, 1955a) on the life-histories of *S. tenue* and of *S. baccatum,* respectively, are perplexing. According to Martin, the cercaria of *S. tenue* has a simple tail with a sticky tip, a stenostomate excretory pattern and a flame-cell formula of 2 (3 + 3 + 3 + 3 + 3 + 3 + 3). According to Wolfgang, the cercaria of *S. baccatum* lacks a stylet and peristomial spines, has a simple tail with a sticky tip, a mesostomate excretory pattern with the pore at the tip of the tail, but the flame-cell pattern was not worked out. Wolfgang noted that the cercaria of *S. baccatum* is distinctly different from that of *S. tenue*. But his observation that the excretory vesicle discharges through a duct which traverses the tail and opens at the tip is so unusual that it can be accepted only after confirmation. Moreover, his description of a mesostomate excretory pattern in the cercaria and a stenostomate arrangement in the metacercaria would necessitate a major alteration in the collecting tubules and suggests that the cercaria and metacercaria belong to different species.

Cercaria dipterocerca differs from the cercaria described by Martin as the larva of *S. tenue* in several important features. It lacks a stylet, has lateral and dorsoventral cuticular fins on the tail, and the flame-cell formula is simpler, 2 (3 + 3 + 3). These differences are far greater than ordinarily encountered between cercariae of species in a single genus and present as yet unresolved problems.

The genus *Stephanostomum* has been assigned to the family Acanthocolpidae but the relationships of that family are uncertain. Most authors have included the Acanthocolpidae in the Allocreadioidea. La Rue (1957) presented a classification of the digenetic trematodes based on life-history data and designed to show genetic relationships. The system was founded primarily on the formation of the excretory bladder, supplemented by other morphological and bionomic data. The Digenea were divided into the Anepitheliocystidia and the Epitheliocystidia. The first group comprised three orders; Strigeatoidea, Echinostomida, and Renicolida, in which the excretory vesicle is thin, membranous, not epithelial at any stage, and in which the cercariae have forked or single tails and the excretory ducts extend into the tails of developing cercariae. In the second group, the excretory vesicle has a primary membranous wall which is replaced by an epithelium derived from a mesodermal cell-mass. It comprises two orders: the Plagiorchiida and the Opisthorchiida. These groups were distinguished by the location of the primary excretory pores, which in the Plagiorchiida are at the furrow between body and tail and in the Opisthorchiida on the lateral margins of the tail, near its base. The order Plagiorchiida contains two superfamilies: the Plagiorchioidea Dollfus, 1930 and the Allocreadioidea Nicoll, 1934. As noted, *Stephanostomum* has been accepted as a member of the Acanthocolpidae in the Allocreadioidea. But in *Stephanostomum* the excretory ducts extend into the tail of the cercaria, which would exclude the genus from the Allocreadioidea and require its transfer to the Opisthorchioidea. Such a disposition would require that the genus be removed from the Acanthocolpidae or the transfer of the entire family. Indeed, such an allocation has been suggested; at the annual Midwest Conference of Parasitologists, Peters reported on the development of the excretory system in an acanthocolpid cercaria and in the mimeographed abstract of the paper stated, "Thus, the Acanthocolpidae must be excluded from the Allocreadioidea and may be closer to the Echinostomatioidea, or possibly to the Opisthorchioidea." At the same meeting, Cable, Peters and Berger discussed the affinities of the Acanthocolpidae and noting substantial agreement with members of the family Campulidae, suggested possible genetic and taxonomic relationship, even inclusion in the same family. Pande (1960) erected a new genus *Brijicola* to contain a new species, *B. caballeroi*, with morphological similarities to a number of genera at present assigned to such different families as Acanthocolpidae Lühe, 1909; Acanthostomatidae Poche, 1926 emend. Nicoll, 1935; Echinostomatidae Looss, 1902 emend. Poche, 1926; Maseniidae Yamaguti, 1953; Heterophyidae Odhner, 1914; and Plagiorchiidae Lühe, 1901 emend. Ward, 1917. The genus was assigned to the Acanthocolpidae with the comment that the present concept of the family remains greatly confused and unsatisfactory.

SUMMARY

The morphology, composition and distribution of the genus *Stephanostomum* are considered. Taxonomic uncertainties and difficulties are discussed. It is postulated that the difficulties can be resolved only with knowledge of life-cycles, larval forms, and developmental stages. Previous accounts of life-histories in the genus are reviewed. The cercariae described by Miller and Northup (1926) from *Nassa obsoleta* at Woods Hole are listed and their life-cycles are traced. *Cercaria dipterocerca* Miller and Northup, 1926 penetrated and encysted in laboratory-reared specimens of *Menidia menidia*. They continued their development and the mature metacercariae manifest such precise agreement in number and shape of peristomial spines and in general morphology with juvenile and mature specimens of *Stephanostomum dentatum* (Linton, 1900) Manter, 1931, that *C. dipterocerca* may be the larval stage of *S. dentatum*. *Cercaria dipterocerca* is very different, however, from the cercariae described by Martin (1939) and Wolfgang (1954, 1955a) as the larvae of *Stephanostomum tenue* and *Stephanostomum baccatum*, respectively. The larvae described by Martin and Wolfgang differ markedly from one another. These differences are far greater than ordinarily encountered between species of a single genus and present as yet unresolved problems. The systematic position of *Stephanostomum* and the family to which it belongs are equivocal. If the genus is a member of the Acanthocolpidae, and if La Rue's

system is valid, the family must be transferred from the Allocreadioidea to the Opisthorchioidea.

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